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Systematic significance of foliar epidermis and tendril morphology in three West African genera of Cucurbitaceae: *Momordica* L., *Luffa* Mill. and *Trichosanthes* L

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Momordica, *Luffa* and *Trichosanthes* are important cucurbitaceous plants whose foliar epidermal characters are sparsely documented. A combined investigation of leaf epidermis and tendrils of the species was carried out with the aid of light and scanning electron microscopy, and visual assessment. All *Momordica* species have hypostomatic leaves except *M. balsamina* whose leaves are amphistomatic. This adds to our knowledge of range of stomatal distribution in *Momordica* which hitherto, is reported hypostomatic. It also raises doubt about the naturalness of Sect. *Momordica*. Only *M. multiflora* is glabrous and *M. angustisepala* alone is pubescent on the epidermal surfaces. Epidermis of *Luffa* is amphistomatic and non-cystolithic whereas, it is hypostomatic and cystolithic in *Trichosanthes*. Tendrils branches arise from the base in *Luffa* (3–4 in number) and *Trichosanthes* (2–3 in number) whereas in *Momordica* they may not branch or are bifurcated, with one being vestigial. These comparative data support classifying the three genera in separate tribes. In particular, characters of the leaf epidermis will assist in identifying the species even when the leaf samples are fragmentary, or when there is a mix-up, the usual state of herbal materials in the African markets.

Keywords: Cucurbitaceae; cuticle; leaf epidermis; microscopy; taxonomy; tendrils

Introduction

The infra-familiar and generic composition in Cucurbitaceae has been reviewed at different times and significant amendments were made (Hutchinson and Dalziel 1958; Jeffrey 1962, 1980, 1990, 2005; Ali et al. 2011; Schaefer and Renner 2011). However, inadequate information on distribution pattern, insufficiency of materials for study and variable morphology of some taxa have been reported as responsible for the limited understanding of certain taxa in this family (Hutchinson and Dalziel 1958; Schaefer and Renner 2010, 2011). In addition, some species from domesticated and wild populations are known to hybridize freely (Schaefer and Renner 2010; Bharathi, Munshi et al. 2012; Guo et al. 2012), leading to polymorphism and increased confusion in taxon identification. Reversal from dioecy to monoecy and vice versa in genera such as *Momordica* L., c. 24 dioecious and 23 monoecious species in Africa (Schaefer and Renner 2010) and genera such as *Luffa* Mill. (Schaefer and Renner 2011) and *Bryonia* L. (Volz and Renner 2008) is another important reason for misidentification in this family.

Many studies focused on the problems above, have improved our knowledge of taxon relationships in Cucurbitaceae, e.g. morphology by Hutchinson and Dalziel (1958), Jeffrey (1962, 1980, 1990, 2005), Schaefer and Renner (2010) and Omar (2009); anatomy by Sawhney (1920), Metcalfe and Chalk (1950, 1979), Ali et al. (2011) and, Aguoru and Okoli (2012); cytology by Bharathi et al. (2011) and molecular studies by Zhang et al. (2006), Kocyan et al. (2007), Ali et al. (2010), Schaefer and Renner (2011), Bharathi, Parida, et al., (2012a) and Guo et al. (2012).

The latest classification by Schaefer and Renner (2011) recognized 15 tribes in the family following the work of Cogniaux (1881) and Jeffrey (2005). *Momordica*, the primary focus of this work, was formerly in the tribe Joliffieae (Jeffrey 2005) but is now placed in the new tribe Momordiceae and recognized as a monophyletic genus (Schaefer and Renner 2011) despite the inclusion of some poorly known species. *Luffa* and *Trichosanthes* L., the secondary concern of the study, are exo-morphologically distinct; but their tribal position is not yet clear. Tribal placement of *Luffa* has been controversial.

Jeffrey (1962, 1980, 1990, 2005) placed *Luffa* in different tribes – Cucurbiteae and Benincaseae at different times but *Trichosanthes* has been consistently placed in Trichosantheae. These genera are now placed in an old tribe – Sicyoeae – based on molecular data (Schaefer and Renner 2011). In view of these changes, we considered leaf epidermis and tendril morphology for possible useful taxonomic data that will enhance sharp discrimination of the taxa.

The genera cannot be identified using fragmented leaf samples because of limited information on the subject and lack of materials to be used as an identification guide. In West Africa, there is an old account on morphology (Hutchinson and Dalziel 1958), limited anatomical information (Metcalfe and Chalk 1950, 1979; Aguoru

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and Okoli 2012) and minimal data on leaf epidermal morphology (Kadiri 2003). This situation has hampered the optimal use of the species in crude drug discovery in spite of the high medicinal potency reported in certain folkloric accounts (Oliver 1960; Agoha 1963; Burkhill 1985). Furthermore, when there is mix-up of leaves due to fragmentation (the condition in which medicinal plants are available in African markets), misidentification of taxa persists. This study therefore, reflects the pattern of inter- and intra-generic relationships in the three genera, so as to contribute useful data that can be combined with other data for a meaningful phylogenetic interpretation. The work also attempts to validate the existing infra-generic classification of *Momordica* by Schaefer and Renner (2011). We addressed these concerns using combined data from tendrils and leaf epidermis correlated on the maximum likelihood phylogenetic tree branches of Schaefer and Renner (2011).

The three genera (*Momordica*, *Luffa* and *Trichosanthes*) are either cultivated or grow in the wild. They have pantropical distribution worldwide (Willis 1966; Schaefer and Renner 2010, 2011) and the species have culinary, medicinal and many other commercial values (Oliver 1960; Agoha 1963; Welihinda et al. 1982; Burkhill 1985; Jiratchariyakul et al. 2001; Grover and Yadav 2004).

Materials and methods

Both herbarium and field specimens were used for the study. Provenances of the herbarium samples are shown in Appendix I. Herbarium abbreviations follow Holmgren et al. (1990). For light microscopy, the approach adopted followed Kadiri (2003), Kadiri and Ayodele (2003), Kadiri et al. (2009) with some modifications. A whole leaf or 1- to 5-cm² portions sectioned from the standard median portion of the lamina (i.e. near the midrib) were examined in three to five specimens. Dried leaves were swollen by boiling in water for 30 minutes, and then soaked in concentrated trioxonitrate (v) acid (HNO_3) in capped specimen bottles for about 2–5 hours to macerate the mesophyll. Tissue disintegration was indicated by bubbles and the epidermis was transferred into Petri dishes containing water for cleansing, after which the surfaces were separated with a pair of forceps and a mounting needle. Tissue debris was cleared off the epidermis with a fine-hair brush and washed in several changes of water. A few drops of a graded series of 50%, 75% and 100% ethanol were added in turn to dehydrate the cells. The preparations were later stained with Safranin O for about 5 minutes before mounting in glycerine on the glass slide. The uppermost surfaces of the epidermis were viewed after covering them with cover-slips and were ringed with nail varnish to prevent dehydration. Assessment of 20 randomly selected epidermal cells and stomata from 10 different microscope fields was carried out.

Line drawings of the epidermis were obtained using a camera lucida drawing apparatus. Photomicrographs were obtained with a digital camera attached to a CE Olympus compound microscope. Images were produced and edited on the computer. The formula for stomatal index of Cutter (1978) was adopted,namely: Stomatal Index (%) = (NS × 100/(ES + NS), where NS is the number of stomata and ES is the number of epidermal cells. Tendrils of all the herbarium specimens were examined while those of other samples were assessed *in situ* in their natural populations. Three morphological characters such as number of branches, point of branching and twisting pattern, whether lax or deep, were studied.

For electron microscopy, small pieces (c. 7 mm^2) of the leaf were fixed on scanning electron microscope stubs with double-sided tape and sputter coated with gold. Specimens were examined and photographed in a Jeol JSM 35 scanning electron microscope.

Results

The seven West African species of *Momordica* in the tribe Momordiceae, were investigated. In the genus, the leaves are hypostomatic in all species except *Momordica balsamina* L. which is amphistomatic (Figure 1C, D; Table 1). The leaves of *Momordica multiflora* Hook.f. are glabrous whereas in other species, they are pubescent (Table 1). The anticlinal walls are undulate on the abaxial surface of all species; although a slightly curved pattern may be found in *Momordica charantia* L. (Figure 1G, H; Table 1) and *Momordica cissoides* Planch. ex Benth. (Figures 2A, B, 3G, H; Table 1). Curved, undulate and straight anticlinal walls were found on the adaxial surface of all species (Table 1). The cell shape is irregular on both surfaces of the epidermis in all species except *Momordica cabraei* (Cogn.) C. Jeffrey, which has polygonal cell shape on the adaxial surface (Figure 1E; Table 1). Stomatal type is generally anomocytic in the genus. The trichome types recorded were long or short conical in *Momordica angustisepala* Harms (Figure 5B; Table 1) and *Momordica foetida* Schumach. (Figure 5H; Table 1) on the adaxial suface, and also in *M. cabraei* (Figure 5D; Table 1) on the abaxial surface (Figure 6F; Table 1). Short conical trichomes were found on the abaxial surface of *M. angustisepala* (Figure 5A, Table 1) and *M. balsamina* (Figure 5C; Table 1). Multicellular conical types occurred on the adaxial surface of *M. charantia* (Figure 5E, Table 1), *M. cissoides* (Figure 5F; Table 1) and *M. foetida* (Figure 5G; Table 1) whereas filiform coiled types were recorded in *M. cissoides* on the abaxial surface (Figure 7D).

Mean cell length varied from 25.5 ± 3.5 on the abaxial surface in *M. charantia* (Table 1) to 58.4 ± 4.2 on the adaxial surface in *M. multiflora* (Table 1). Mean width of the cells ranged from 15.3 ± 3.0 in *M. charantia* to 35.7 ± 3.1 in *M. multiflora*, all on the adaxial surface. *Momordica multiflora* has the largest cells in the genus

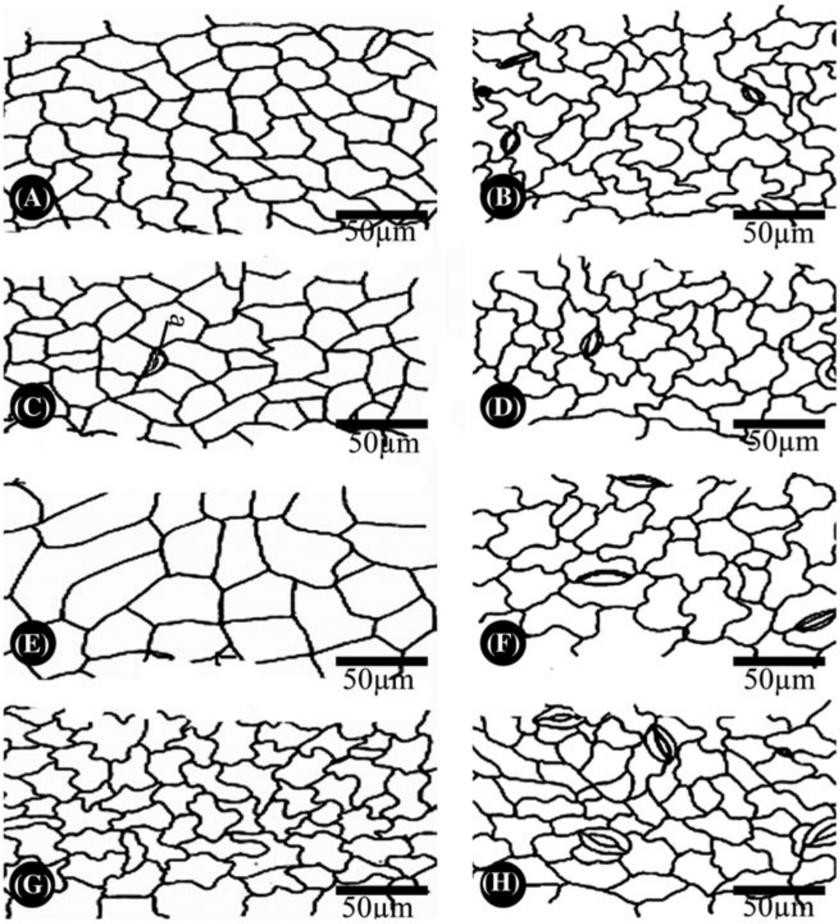

Figure 1. Leaf epidermal characters of West African species of *Momordica*. **(A, C, E, G)** Adaxial surfaces. **(B, D, F, H)** Abaxial surfaces. **(A, B)** *Momordica angustisepala*; **(C, D)** *Momordica balsamina*, a = stoma on the adaxial surface; **(E, F)** *Momordica cabraei*; **(G, H)** *Momordica charantia*.

(Table 1). There are more cells per square millimetre on the adaxial than abaxial surface of the epidermis in *M. balsamina* (Figure 1C, D; Table 1), *M. charantia* (Figure 1G, H; Table 1) and *M. foetida* (Figures 2C, D, 3K, L; Table 1). On the abaxial surface, mean stomatal size varied from 15.2 ± 5.0 by 8.8 ± 1.4 in *M. balsamina* to 23.5 ± 4.0 by 8.6 ± 2.0 in *M. cabraei* (Table 1). On the abaxial surface, the highest number of stomata per square millimetre (173) was recorded in *M. foetida* on the abaxial surface (Table 1) whereas the lowest value of 83 stomata per square millimetre was obtained in *M. balsamina* (Table 1). In the genus, stomatal index varies from 2.1% to 14.3% (Table 1).

The periclinal wall is either conspicuous or inconspicuous. It is conspicuous on both surfaces of *M. charantia* (Figure 6G, Table 2) and *M. multiflora* (Figure 7C, Table 1); inconspicuous on both surfaces of *M. balsamina* (Figure 6C, D; Table 1) and *M. foetida* (Figure 7C, D; Table 1). It may be conspicuous or inconspicuous on either surface of the epidermis of other species (Table 2). The epicuticular wax usually appeared as a continuous thin sheet on the epidermis in most species (Table 1). In *M. angustisepala*, the wax may be clustered on the adaxial surface (Figure 6A, Table 2) or occur as flakes on the abaxial surface (Figure 6B, Table 2). The stomatal orientation may be sunken as observed in *M. balsamina* (on both surfaces) (Figure 6C, D; Table 1), *M. charantia* (Figure 6H; Table 2), *M. cissoides* (Figure 7B, Table 2) or superficial as recorded in *M. angustisepala* (Figure 6B, Table 1), *M. cabraei* (Figure 6F, Table 2), *M. foetida* (Figure 7D, Table 2) and *M. multiflora* (Figure 7F, Table 2). Cuticular striations are lacking in the species except *M. cabraei* on the abaxial surface (Figure 6F, Table 2) and *M. multiflora* (Figure 7F, Table 2). Peristomatal rim is narrow in all species except in *M. multiflora* (Figure 7F, Table 2) and *M. angustisepala* (Figure 6B, Table 2) where it is wide or narrow to wide, respectively. Cuticular surface is either rough or smooth in the genus (Figures 6 and 7, Table 2).

In Sicyoeae, we only considered the single species of *Luffa* and *Trichosanthes* that are common in West Africa. In *Trichosanthes cucumerina*, cystoliths were encountered (Figure 3D, E). Epidermal cells may be undulate

Table 1. Qualitative and quantitative leaf epidermal characteristics of the West African species of *Momordica, Luffa and Trichosanthes.*

Species	Anticlinal wall pattern	Epidermal cell shape	Epidermal cell length (μm)	Epidermal cell width (μm)	Mean cell No. / mm²	Stomatal length (μm)	Stomatal width (μm)	Stomatal No. / mm²	Stomatal index (%)	Trichomes
M. angustisepala (Ad)	Cur	Irr	33.6 (44.1±5.0) 54.6	15.0 (23.0±3.0) 30.5	986	–	–		–	LCT
(Ab)	Und	Irr	32.0 (39.5±2.0) 47.0	14.8 (16.4±4.0) 25.0	1543	14.0 (14.8±2.0) 15.5	5.3 (7.1±1.8) 8.8	102	6.2	SCT
M. balsamina (Ad)	Cur	Irr	34.8 (41.5±2.0) 48.6	16.0 (17.6±3.0) 19.3	1369	6.4 (6.8±1.1) 7.5	1.8 (2.2±0.6) 2.5	30	2.1	Absent
(Ab)	Und	Irr	16.0 (36.5± 3.0) 55.5	13.5 (22.1±3.0) 30.8	1240	14.0 (15.2±5.0) 16.3	7.0 (8.8±1.4) 10.5	83	6.3	SCT
M. cabraei (Ad)	Str	Pol	32.0 (47.0±3.0) 62.0	17.5 (24.5±5.0) 31.5	868	–	–		–	Absent
(Ab)	Und	Irr	20.0 (28.0±2.0) 36.0	15.5 (22.0±4.0) 28.5	1623	18.0 (23.5±4.0) 28.0	6.8 (8.6±2.0) 9.3	202	11.1	LCT
M. charantia (Ad)	Und	Irr	19.0 (31.3±4.0) 43.5	10.0 (15.3±3.0) 21.5	2088	–	–		–	MCT
(Ab)	Curv-und	Irr	15.0 (25.5±3.5) 36.0	12.5 (21.4±1.2) 31.2	1832	14.0 (20±4.2) 22.0	7.0 (8.4±1.2) 9.8	167	8.4	Absent
M. cissoides (Ad)	Und	Irr	25.0 (41.0±3.3) 57.0	14.0 (23.0±3.2) 32.0	1060	–	–		–	MCT
(Ab)	Cur-und	Irr	15.0 (31.9±6.3) 48.8	12.0 (19.4±4.1) 26.8	1616	12.0 (15.2±1.7) 18.3	7.0 (8.3±1.5) 9.5	124	7.1	Absent
M. foetida (Ad)	Und	Irr	21.5 (37.8±2.1) 56.0	11.0 (17.0±3.0) 28.0	1556	–	–		–	LCT, MCT
(Ab)	Und	Irr	22.5 (36.0±3.0) 48.5	17.5 (26.8±2.1) 36.3	1036	12.5 (20.3±1.8) 28.0	7.0 (9.8±2.1) 12.5	173	14.3	Absent
M. multiflora (Ad)	Cur	Irr	43.8 (58.4±4.2) 73.0	22.8 (35.7±3.1) 48.5	480	–	–		–	Absent
(Ab)	Und	Irr	34.0 (51.2±2.4) 68.4	10.5 (21.5±2.1) 32.0	908	14.0 (22.8±2.8) 31.5	7.0 (7.5±2.1) 8.9	130	12.5	Absent
Luffa aegyptiaca (Ad)	Str	Pol	25.0 (30.0±2.1) 45.0	15.0 (21.0±3.0) 27.0	1587	10.0 (13.6±0.8) 17.2	5.0 (6.5±1.1) 8.0	227	12.5	LCT
(Ab)	Cur	Irr	12.5 (21.0±3.0) 30.0	10.5 (20.0±2.1) 28.3	2381	12.5 (20.3±1.8) 28.0	7.0 (9.8±2.1) 12.5	397	14.3	LCT
Trichosanthes (Ad) *cucumerina*	Und	Irr	28.8 (45.1±4.2) 62.0	18.5 (29.0±3.2) 38.5	765	–	–		–	LCT, MCT
(Ab)	Und	Irr	20.0 (43.0±2.2) 65.4	10.0 (14.0±1.6) 18.0	1661	15.0 (21.8±1.8) 28.7	3.0 (4.1±0.7) 5.3	415	20	LCT, MCT

Notes: Ab, abaxial surface; Ad, adaxial surface; Cur, curved; Cur-und, curved-undulate; Irr, irregular; LCT, long conical trichomes; MCT, multicellular conical trichomes; Pol, polygonal; SCT, short conical trichomes; Str, straight.

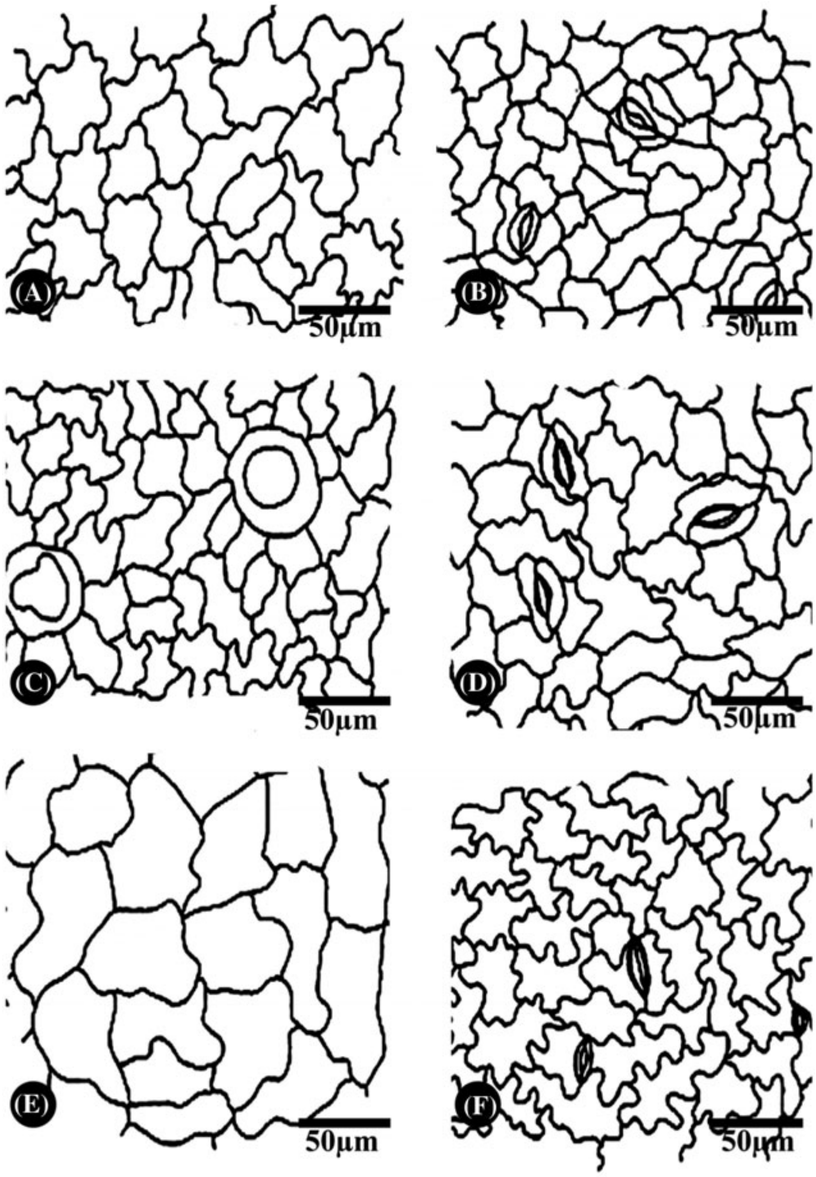

Figure 2. Leaf epidermal characters of West African species of *Momordica*. **(A, C, E)** Adaxial surfaces. **(B, D, F)** Abaxial surfaces. **(A, B)** *Momordica cissoides*; **(C, D)** *Momordica foetida*; **(E, F)** *Momordica multiflora.*

on both surfaces of *T. cucumerina* (Figure 3D, E; Table 1) or straight on the adaxial surface and curved on the other layer in *Luffa aegyptiaca* Mill. (Figure 3A, B; Table 1). The cell shape is irregular on both surfaces of the epidermis except in *L. aegyptiaca*, where the adaxial surface has polygonal epidermal cells (Table 1). Larger cells were recorded in *T. cucumerina* L. than *L. aegyptiaca* (Table 1). Generally, there are more epidermal cells per square millimetre on the abaxial than adaxial surface (Table 1). The leaves of *L. aegyptiaca* are amphistomatic (Figure 3A, B; Table 1) but they are hypostomatic in *T. cucumerina* (Figure 3E, Table 1). Stomata are larger in *T. cucumerina* than *L. aegyptiaca* (Table 1). Stomatal index varies from 12.5% to 20% between the two genera. The two species have conical trichomes which may be long (Figures 5I–K, 7H; Table 1) or bent and warty on the surface (Figure 7G) in *L. aegyptiaca*.

In *Momordica*, the tendrils may be laxly or deeply twisted. They may be branched or not branched (Figures 3 and 4; Table 3). When branched, one of the branches is vestigial; it is morphologically different in size and twisting pattern. This condition was recorded in *M. multiflora* (Figure 4G, Table 3) and *M. cabraei* (Figures 3J, 4C, Table 3). In *L. cylindrica*, the tendrils may have up to four branches emanating from the base and they are laxly twisted (Figure 3C). Tendrils of *T. cucumerina* are deeply twisted, having up to three branches (Figure 3F).

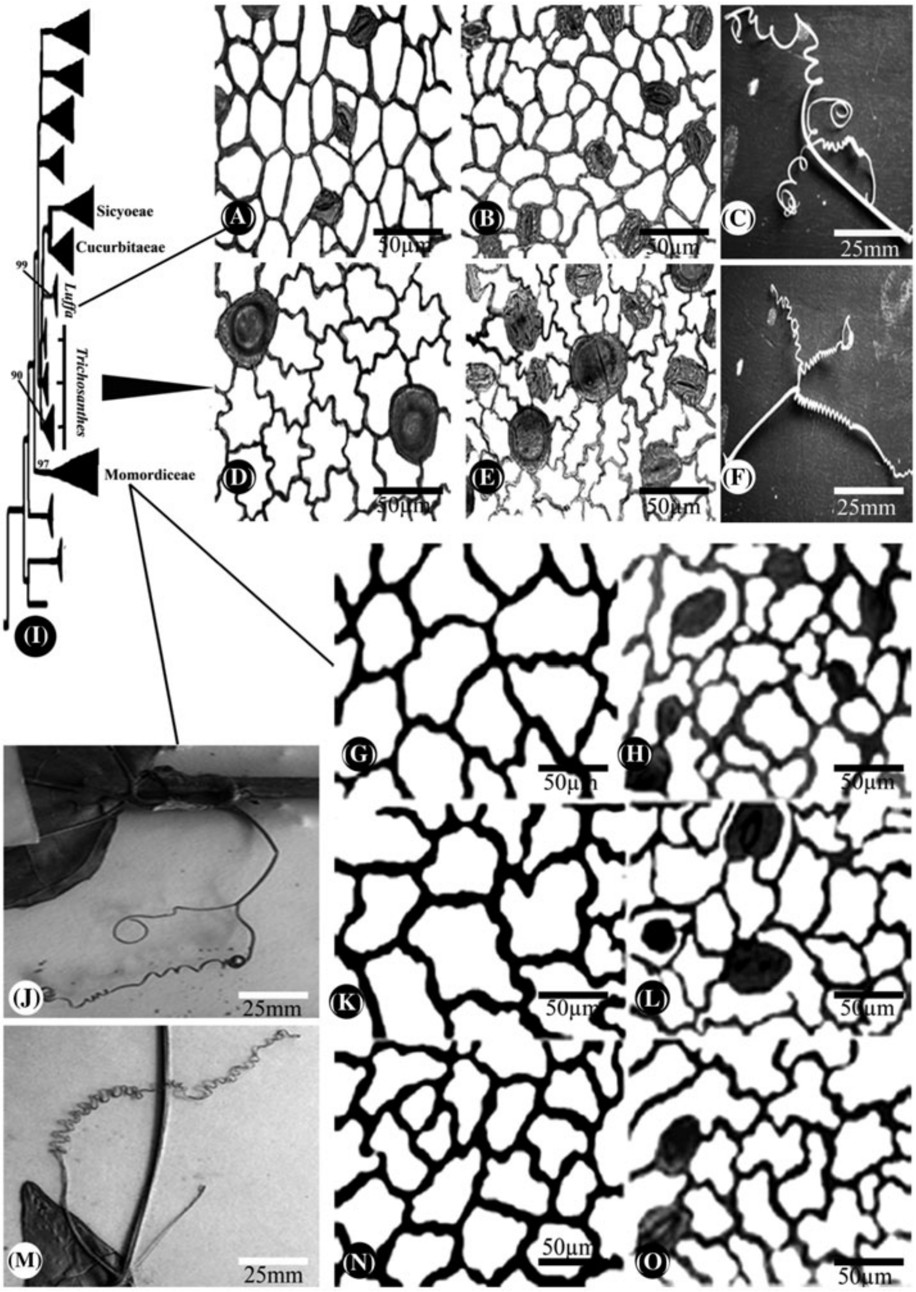

Figure 3. Combined leaf epidermis and tendrils characters correlated on the maximum likelihood phylogenetic tree branches of Schaefer and Renner (2011). **(A, D, G, K, N)** Adaxial surfaces. **(B, E, H, L, O)** Abaxial surfaces. **(C, F, J, M)** Tendrils. **(I)** Branches of maximum likelihood phylogenetic tree. **(A–C)** *Loffa aegyptiaca*, **(D–F)** *Trichosanthes cucumerina*, **(G, H)** *Momordica cissoides*; **(K, L)** *Momordica foetida*; **(N, O)** *Momordica multiflora*. **(J, M)** Types of tendrils found in *Momordica* **(J)** *Momordica cabraei*, **(M)** *Momordica angustisepala*.

Discussion

Some taxonomically useful epidermal features were recorded in the genus *Momordica*. The characters that are good for species diagnosis include amphistomatic leaves found only in *M. balsamina*. This observation opposes the report of Metcalfe and Chalk (1950, 1979), where stomata are reportedly confined to the abaxial surface in the genus. Other diagnostic characters are polygonal cells on the adaxial surface of *M. cabraei*, pubescent adaxial and abaxial surfaces in *M. angustisepala* and, glabrous adaxial and abaxial surfaces in *M. multiflora.* Epidermal features that are useful for generic discrimination include irregular cell shape, anomocytic stomata, inconspicuous periclinal walls on the abaxial surface, epicuticular wax that covers epidermis like a sheet, rough cuticular surface on the adaxial surface and stomatal index that is not more than 20%. Although these features are known to be influenced by some environmental factors, their value in making taxonomic decisions cannot be under-estimated (Davis and

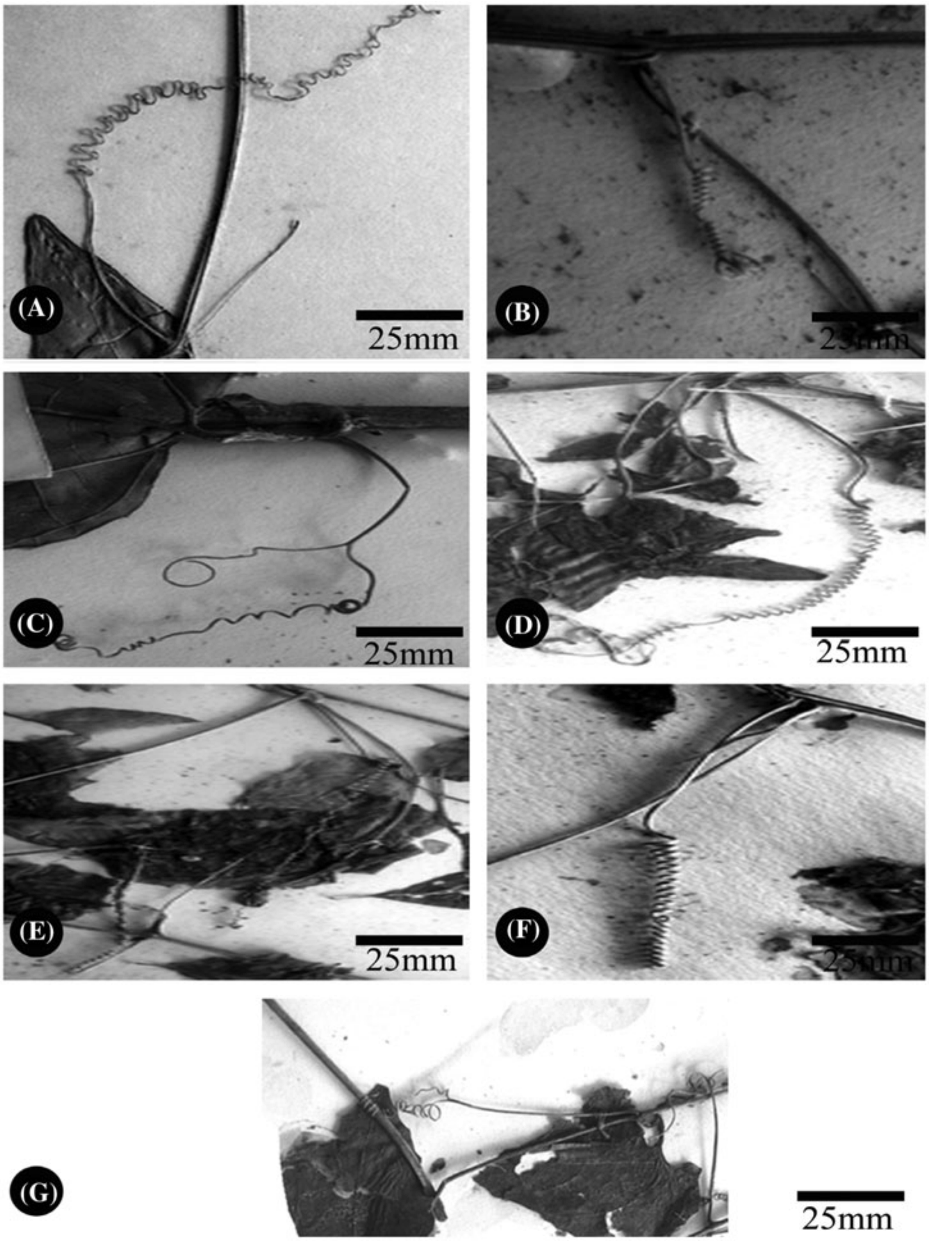

Figure 4. Tendrils of the West African *Momordica* species showing branching patterns. **(A, B, D–F)** show tendrils without branches. **(C, G)** show tendrils with branches. **(A)** *Momordica angustisepala*, **(B)** *Momordica balsamina*, **(C)** *Momordica cabraei*, **(D)** *Momordica charantia*, **(E)** *Momordica cissoides*, **(F)** *Momordica foetida*, **(G)** *Momordica multiflora*.

Heywood 1963; Stace 1965; Inamdar and Gangadhara 1977; Ali and Al-Hemaid 2011). Similarly, the branching and twisting patterns of tendrils may also offer some assistance to generic delimitation. In *Momordica*, tendrils are either intact (i.e. without branching) or bifurcated at the middle. Twisting may be deep or lax in the genus. In *Luffa* and *Trichosanthes*, branching of tendrils is basal but twisting pattern is as found in *Momordica* – deep or lax. Tendrils are known to offer some taxonomically useful characters among arid cucurbitaceous plants (Omar 2009).

In Cucurbitaceae, tendrils are either simple or variously branched. According to Sawhney (1920), they are thigmotropic structures, which may develop from extra-axillary or any part or all of a stem, leaf or petiole; and they receive their vascular supply from leaf trace and cauline bundles. A combination of both epidermal and tendril characters also supports the sections recognized in *Momordica* by Schaefer and Renner (2011). Section *Momordica* is heterogeneous; it is represented in the study by *M. balsamina*, *M. charantia* and *M. foetida* unlike in the other four sections where one species is represented. *Momordica balsamina* have amphistomatic leaves unlike the other species, which are hypostomatic, the usual type in the genus (Metcalfe and Chalk 1950, 1979). *Momordica balsamina* occurs chiefly in the dry

Table 2. Qualitative leaf cuticular characteristics of the West African species of *Momordica*, *Luffa* and *Trichosanthes.*

Species	Periclinal wall pattern	Nature of epicuticular wax	Stomatal orientation	Cuticular striations	Peristomatal rim	Cuticular surface
M. angustisepala Ad.	Conspicuous	Clustered	No stoma	Absent	No stoma	Rough
Ab.	Inconspicuous	Flaky	Superficial	Absent	Wide	Rough
M. balsamina Ad.	Inconspicuous	Thin sheet	Sunken	Absent	Narrow	Rough
Ab.	Inconspicuous	Thin sheet	Sunken	Absent	Narrow	Rough
M. cabraei Ad.	Conspicuous	Thin sheet	No stoma	-	No stoma	Rough
Ab.	Inconspicuous	Thin sheet	Superficial	Present to Absent	Narrow to wide	Smooth
M. charantia Ad.	Conspicuous	Thin sheet	No stoma	Absent	No stoma	Rough
Ab.	Conspicuous	Thin sheet	Sunken	Absent	Narrow	Rough
M. cissoides Ad.	Conspicuous	Thin sheet	No stoma	Absent	No stoma	Smooth
Ab.	Inconspicuous	Thin sheet	Sunken	Absent	Narrow	Smooth
M. foetida Ad.	Inconspicuous	Thin sheet	No stoma	Absent	No stoma	Rough
Ab.	Inconspicuous	Thin sheet	Superficial	Absent	Narrow	Rough
M. multiflora Ad.	Conspicuous	Thin sheet	No stoma	Present	No stoma	Rough
Ab.	Inconspicuous	Thin sheet	Superficial	Present	Wide	Rough
L. aegyptiaca Ad	Inconspicuous	Thin sheet	No stoma	Absent	No stoma	Rough
Ab	NA	NA	NA	NA	NA	NA
T. cucumerina Ad	Inconspicuous	Thin sheet	No stoma	Absent	No stoma	Rough
Ab	NA	NA	NA	NA	NA	NA

Notes: Ab, abaxial surface; Ad, adaxial surface; LCU, long, conical and unicellular; NA, not available; SCG, short curved and glandular; SCT, short conical trichomes. Cuticular data on *Luffa and Trichosanthes* were obtained from Ali and Al-Hemaid (2011).

areas of the tropics, found in northern Nigeria and Sudan; and arid areas of India (Hutchinson and Dalziel 1958; Bharathi et al. 2011). Other species in the section occur in moist areas. Distribution of stomata on leaf surfaces is under the influence of environmental factors, yet features of the stomata can still offer useful taxonomic information because their expression is under a strong genetic control (Davis and Heywood 1963; Stace 1965).

Furthermore, *M. balsamina* can be separated from other species by its bracts that closely subtend the flowers and possession of coarsely lobulate–dentate leaves (Hutchinson and Dalziel 1958). Whether or not to retain *M. balsamina* in this section is a future question that would have to be addressed with additional data from gross morphology, anatomy and molecular studies that will use many taxonomically informative genetic markers. Given that other sections have one species each; their sectional grouping is accepted due to lack of conflicting data. Therefore, this work presents some of the features that are characteristic of sections in *Momordica*.

Luffa and *Trichosanthes* are well supported as separate genera based on the examined leaf epidermal and tendril features. Cystoliths and undulate anticlinal walls found on both surfaces of the epidermis of *T. cucumerina* are unique to the species. *Luffa aegyptiaca* has polygonal cells on the adaxial surface and the leaves are amphistomatic; whereas they are hypostomatic in *T. cucumerina*.

Based on the features studied, *Luffa* is closer to *Momordica* than *Trichosanthes*. *Luffa aegyptiaca* has similar features, such as polygonal cells on the adaxial surface with *M. cabraei* and hypostomatic leaves with

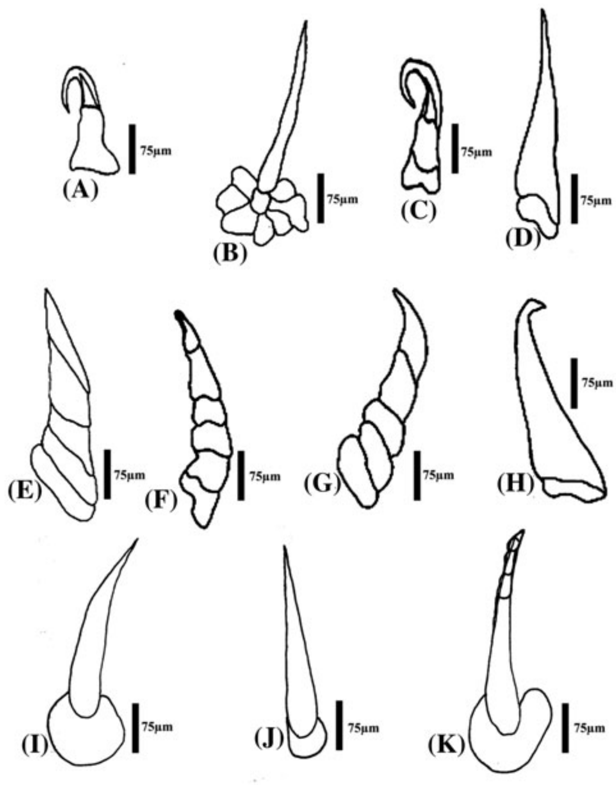

Figure 5. Trichomes types found among the taxa. **(A)** Abaxial surface and **(B)** adaxial surface of *Momordica angustisepala*; **(C)** *Momordica balsamina* (abaxial surface); **(D)** *Momordica cabraei* (abaxial surface); **(E)** *Momordica charantia* (adaxial surface). **(F)** *Momordica cissoides* (adaxial surface); **(G, H)** *Momordica foetida* (adaxial surface); **(I)** *Luffa aegyptiaca* (both surfaces); **(J, K)** *Trichosanthes cucumerina* (Both surfaces).

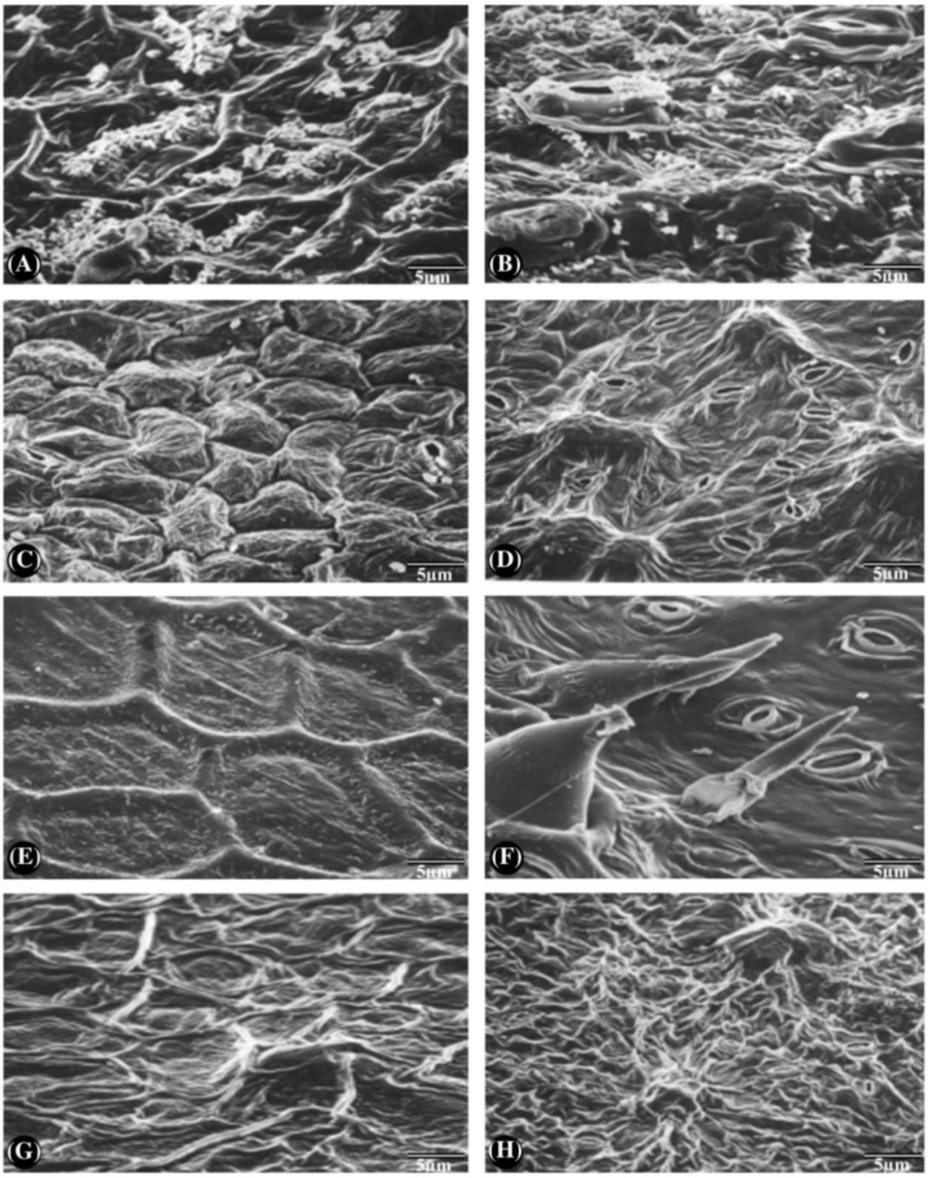

Figure 6. Scanning electron micrographs of leaf epidermis of West African species of *Momordica*. **(A, C, E, G)** Adaxial surfaces. **(B, D, F, H)** Abaxial surfaces. **(A, B)** *Momordica angustisepala*; **(C, D)** *Momordica balsamina*; **(E, F)** *Momordica cabraei*; **(G, H)** *Momordica charantia*.

M. balsamina. But it is different from these species by having a higher number of epidermal cells per square millimetre on both surfaces and higher stomatal index values. It can also be distinguished by the presence of the same type of trichomes: long conical on both surfaces of the epidermis and presence of rough cuticular surface on both surfaces. In addition, tendrils of *Momordica* only divide mid-way if at all; whereas division which may be up to four is basal in *Luffa*. On the other hand, *Luffa* and *Trichosanthes* have tendrils that are branched at the base, three or four branches in *Luffa* and up to three branches in *Trichosanthes*. There are cystoliths on both surfaces of the epidermis of *T. cucumerina* that are lacking in other genera. The leaf epidermis of *Luffa* and *Trichosanthes* shares a suite of similar characters more than with *Momordica*; e.g. irregular cell shape on the abaxial surface, similar trichome types on both surfaces of the leaf, inconspicuous periclinal walls and rough cuticular surfaces (Ali and Al-Hemaid 2011). Therefore, it is reasonable to conclude that *Momordica* and *Luffa* are distant from each other based on the facts contained herein. In contrast, the closeness of *Trichosanthes* and *Luffa* shown in this work supports the suggestion by Schaefer and Renner (2011) to place them in a single tribe – Sicyoeae – while the differences lend support to the position of Jeffrey (2005) and Kocyan et al. (2007), where the genera are placed in separate tribes. An artificial indented dichotomous key that can be used to delimit the taxa, based on the data reported, is presented below.

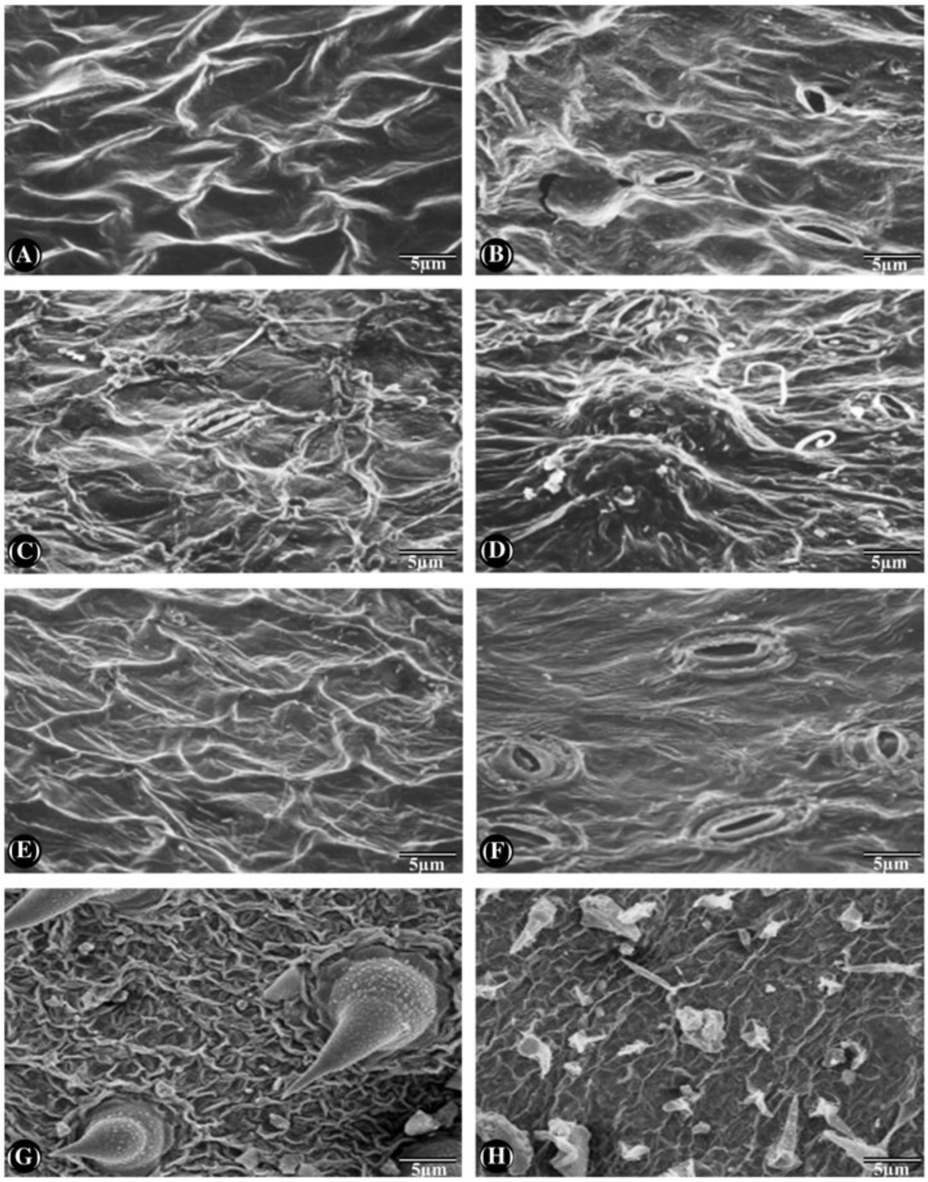

Figure 7. Scanning electron micrographs of leaf epidermis of West African species of *Momordica*, *Lagenaria* and *Trichosanthes*. **(A, C, E, G, H)** Adaxial surfaces. **(B, D, F)** Abaxial surfaces. **(A, B)** *Momordica cissoides*; **(C, D)** *Momordica foetida*; **(E, F)** *Momordica multiflora*; **(G)** *Luffa aegyptiaca*; **(H)** *Trichosanthes cucumerina*. G and H were obtained from Ali and Al-Hemaid (2011).

1. Tendril branches originating from the base, 2-4 in number…………………………………**Tribe Sicyoeae**
2. Leaf amphistomatic, cell shape polygonal on the adaxial surface………….......................... *Luffa aegyptiaca*
2. Leaf hypostomatic, cell shape irregular on the adaxial surface.........................………*Trichosanthes cucumerina*
1. Tendril branches arising mid-way, 1-2 in number……
………………………………….…...**Tribe *Momordiceae***
3. Stomata sunken……………..………………...............4
4. Leaf amphistomatic……….……….........*M. balsamina*
4. Leaf hypostomatic……………………..……………...3
5. Cuticular surface of epidermis rough on both layers, more cells on the adaxial than abaxi surface………
…………..…………………………………*M. charantia*
5. Cuticular surface of epidermis smooth on both layers, more cells on the abaxial than adaxial surface……
…………………………...…..……......*M. cissoides*
3. Stomata superficial………………..……………..........6
6. Cuticular striations equivocal……….……………….7
7. Cell shape polygonal on adaxial surface......*M. cabraei*
7. Cell shape irregular on adaxial surface.....……………...8
6. Cuticular striations absent or present………..….........8
8. Leaf pubescent……………………..…………………9
9. Trichomes present on both surfaces of epidermis….………………………………...*M. angustisepala* 9
9. Trichomes restricted to adaxial surface only……………………………………….……... *M. foetida*
8. Leaf glabrous…………………………….……*M. multiflora*

Table 3. Validation of sectional classification of *Momordica* with some leaf epidermal and tendril characters.

Common features	Section Cissoides	Section Multiflora	Section Angustisepala	Section Momordica	Section Dimorphochlamys
	M. cissoides	*M. multiflora*	*M. angustisepala*	*M. balsamina* *M. charantia*, *M. foetida*	*M. cabraei*
Leaf epidermis	Multicellular conical trichomes, smooth cuticular surface on both sides of the epidermis	Absence of trichomes, presence of cuticular striations on both sides of the epidermis	Trichomes present on both sides of the epidermis	Cell shape is irregular on both sides of the epidermis; more cells are on the adaxial epidermis than the abaxial surface; cuticular surface is rough; narrow peristomatal rim. Unlike other species, *M. balsamina* is amphistomatic	Cell shape is polygonal on the adaxial surface of epidermis; more cells on the abaxial surface than adaxial side of the epidermis; peristomatal rim narrow to wide on the abaxial surface
Tendrils	Lax twisting, no branch	Lax twisting, two branches	Lax twisting, no branch	Deep twisting, no branch	Lax twisting, two branches

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Disclosure statement

No potential conflict of interest was reported by the authors.

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References

Agoha RC. 1963. Medicinal plants of Nigeria. Offset Drukkery, Nijmegen. The Netherlands.

Aguoru CU, Okoli BE. 2012. Comparative stem and petiole anatomy of West African species of *Momordica L* (Cucurbitaceae). Afr J Plant Sci. 6:403–409.

Ali AM, Al-Hemaid FMA. 2011. Taxonomic significance of trichomes micromorphology in cucurbits. Saudi J Biol Sci. 18:87–92.

Ali AM, Karuppasamy S, Al-Hemaid FM. 2010. Molecular phylogenetic study of *Luffa tuberosa* (Roxb.) (Cucurbitaceae) based on internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA and its systematic implication. Int J Bioinf Res. 2:42–60.

Bharathi LK, Munshi AD, Vinod C, Chandrashekaran S, Behera TK, Das AB, John KJ, Vishalnath. 2011. Cytotaxonomical analysis of *Momordica* L. (Cucurbitaceae) species of Indian occurrence. J Genet. 90:21–30.

Bharathi LK, Parida SK, Munshi AD, Behera TK, Raman KV, Mohapatra T. 2012. Molecular diversity and phenetic relationship of *Momordica* spp. of Indian occurrence. Genet Resour Crop Evol. 59:937–948.

Bharathi LK, Munshi AD, Behera TK, Raman KV, John KJ, Das AB, Bhat KV, Sidhu AS. 2012. Production and preliminary characterization of inter-specific hybrids derived from *Momordica* species. Current Sci. 103:178–186.

Burkhill HM. 1985. Useful plant of West Tropical Africa. Royal Botanic Gardens, Kew.

Cogniaux A. 1881. Cucurbitaceae. In: de Candolle A, de Candolle C, editors. Monographiae phanerogamarum. vol 3. Paris: Masson; p. 325–1008.

Cutter EG. 1978. Plant anatomy: Experiment and interpretation of cells and tissues. London: Edward Arnold Publishers.

Davis PH, Heywood VH. 1963. Principles of Angiosperm Taxonomy. Edinburgh: Oliver and Boyd.

Grover JK, Yadav SP. 2004. Pharmacological actions and potential uses of Momordica charantia: a review. J Ethnopharmacol. 93:123–132.

Guo D, Zhang J, Xue Yand Hou X 2012 Isolation and characterization of 10 SSR markers of *Momordica charantia* (Cucurbitaceae)[1] Am J Bot. e182–e183.

Holmgren PK, Keuken W, Schofield EK. 1990. Index Herbariorum: Part 1: The Herbaria of the world. 8th edn. Regnum Vegetabile volume 120. New York Botanical Garden, The Bronx, New York.

Hutchinson J, Dalziel JM. 1958. Flora of West Tropical Africa. London: Crown Agents for Overseas Governments and Administrations.

Inamdar JA, Gangadhara M. 1977. Studies on the trichomes of some Euphorbiaceae. Feddes Repert. 88:103–111.

Jeffrey C. 1962. Notes on Cucurbitaceae, including a proposed new classification of the family. Kew Bulletin. 15:337–371.

Jeffrey C. 1980. A review of the Cucurbitaceae. Bot J Linn Soc. 81:233–247.

Jeffrey C. 1990. Appendix: An outline classification of the Cucurbitaceae. In: Bates DM, Robinson RW and Jeffrey C, editors. Biology and utilization of the Cucurbitaceae. Ithaca, New York: Comstock Publication Associates, Cornell University Press; p. 449–463.

Jeffrey C. 2005. A new system of Cucurbitaceae. Bot Zhurn. 90:332–335.

Jiratchariyakul W, Wiwat C, Vongsakul M, Somanabandhu A, Leelamanit W, Fujii I, Suwannaroj N, Ebizuka Y. 2001. HIV Inhibitor from Thai Bitter Gourd. Planta Med. 67:350–353.

Kadiri AB. 2003. Foliar epidermal morphology of the medicinal genus *Momordica* in Nigeria. Nig J Sci. 37: 25–33.

Kadiri AB, Ayodele AE. 2003. Comparative leaf micromorphological characters of the Nigerian species of *Rauvolfia* Linn. (Apocynaceae). Biosci Res Comm. 15: 35–41.

Kadiri AB, Olowokudejo JD, Ogundipe OT. 2009. Leaf epidermis morphology of West African species of the genus *Acalypha* (Euphorbiaceae). Bot Lith. 15:65–78.
Kocyan A, Zhang LB, Schaefer H, Renner SS. 2007. A multi-locus chloroplast phylogeny for the Cucurbitaceae and its implications for character evolution and classification. Mol Phylogenet Evol. 44:553–577.
Metcalfe CR, Chalk L. 1950. Anatomy of the Dicotyledons. Oxford: Oxford University Press.
Metcalfe CR, Chalk L. 1979. Anatomy of the Dicotyledons. Oxford: Oxford University Press.
Oliver B. 1960. Medicinal Plants in Nigeria. Nigeria College of Arts. Science and Technology.
Omar AA. 2009. Some Morphological Structural Studies of Cucurbitaceous Tendrils under Arid Conditions. Pak J Biol Sci. 12:286–290.
Sawhney KD. 1920. The vascular connection and the structures of the tendrils in some Cucurbitaceae. J Indian Bot Soc. 1:254–262.
Schaefer H, Renner SS. 2010. A three-genome phylogeny of *Momordica* (Cucurbitaceae) suggests seven returns from dioecy to monoecy and recent long-distance dispersal to Asia. Mol Phylogenet Evol. 54:553–560.
Schaefer H, Renner SS. 2011. Phylogenetic relationships in the order Cucurbitales and a new classification of the gourd family (Cucurbitaceae). Taxon. 60:122–138.
Volz SM, Renner SS. 2008. Hybridization, polyploidy, and evolutionary transitions between monoecy and dioecy in *Bryonia* (Cucurbitaceae). Am J Bot. 95:1297–1306.
Welihinda J, Arvidson G, Gylfe E, Hellman B, Karlsson E. 1982. The insulin-releasing activity of the tropical plant: *Momordica charantia*. Acta Biol Med Ger. 41:1229–1240.
Willis JC. 1966. A dictionary of the flowering plants and ferns. Cambridge: The University Press.
Zhang LB, Simmons MP, Kocyan A, Renner SS. 2006. Phylogeny of the Cucurbitales based on DNA sequences of nine loci from three genomes: implications for morphological and sexual system evolution. Mol Phylogenet Evol. 39:305–322.

Appendix I. Exsiccate data of the plants samples examined for the study.

Species	Name of collector	Date of collection	Herbarium No.
M. angustisepala Harms	*M. G. Latilo*	15. 7.1959	FHI 43453
	,,	April, 1971	FHI 64749
	Jones and Stapfield	10.7.46	FHI 18837
	C. F. A. Onochie	22.9.44	FHI 7699
	,,	20.11.58	FHI 35230
	,,	26.4.47	FHI 21986
	L. G. Chizea	1.8.50	FHI 23997
	J. A. Emwiogbon	28.3.69	FHI 23997
	J. F. Redhead	10.8.64	FHI 55957
	R. W. J. Keay	4.7.58	FHI 37672
	,,	7.4.45	FHI 8286
	J. B. Hall	22.5.71	FHI 69618
	J. Olorunfemi	7.6.58	FHI 38051
	Kadiri A. B.	27.10.06	LUH 584
M. balsamina L.	*C. F. A. Onochie*	18. vi. 1947	FHI 23355
	M. C. Clintock	7.12.54	FHI 38960
	P. N. Leeuw., Tuley and Oche	20.3.67	FHI 17909
M. cabraei (Cogn.) C. Jeffrey	*C. F. A. Onochie*	7. 3.1957	FHI 36482
	R. W. J. Keay and A. P. D. Jones	28.10.45	FHI 13778
	Ogan	22.4.66	FHI 58290
	R. Germain	30.11.48	FHI 18577
	J. Redhead	3.12.62	FHI 45610
	J. Redhead	2.3.63	FHI 47570
	M. G. Latilo	18.12.59	FHI 43812
	A. Binuyo and H. D. Onyeachusim	10.2.66	FHI 57885
	R. W. J. Keay and R. D. Meikle	18.2.50	FHI 25664
	B. O. Daramola	1.2.78	FHI 85204
	J. Olorunfemi	3.1.78	FHI 91922
	T. K. Odewo et al.	8.8.84	FHI 101725
	D. P. Stanfield	21.2.62	FHI 45610
M. charantia L.	*C. Ayelotan*	18. 2. 2008	FHI 108020
	Balogun Akeem	7.2.2004	FHI 106632
	Adebambo A. A.	25.10.2007	FHI 108176
	Oguntayo and Adejinmi	9.6.77	FHI 83680
	J. Redhead	20.11.62	FHI 46390
	Thomas R. H	17.10.49	FHI 27022
	,,	28.10.49	FHI 27037
	C. F. A. Onochie	13.10.55	FHI 34910
	,,	June 1955	FHI 38575
	C. F. A. Onochie, Ekwuno and others	15.8.78	FHI 87638
	Tekobo A. M.	8.12.2003	FHI 106489
	Emwiogbon J. A	20.1.65	FHI 55864
	,,	18.7.67	FHI 60083
	,,	28.6.67	FHI 60113
	,,	17.4.72	FHI 33139
	,,	21.11.59	FHI 43858
	,,	25.8.67	FHI 60107
	Emwiogbon J. A and Osanyinlusi	15.10.77	FHI 87360
	H. J. Killick	Sept. 1955	FHI 39242
	D. P. Stanfield	12.5.60	FHI 52405
	D. W. Lawlor and Hall J. B.	15.8.62	FHI 18456
	Z. O. Gbile	20.4.78	FHI 84263
	J. C. Okafor and J. A. Emwiogbon	7.7.66	FHI 40969
	D. Gledhill	9.5.66	FHI 14305
	G. J. H. Amshoff	22.4.59	FHI 51156
	J. Olorunfemi and Oguntayo	Nov. 1977	FHI 86704
	Olorunfemi and others	19.9.78	FHI 88308
	,,	31.10.81	FHI 96535
	J. P. M. Brenan	16.2.48	FHI 39376
	J. Lowe	30.5.25	FHI 77535
	Z. O. Gbile and Oni	18.1.77	FHI 79050
	J. K. Morton	7.11.52	FHI 48659
	A. P. D. Jones	28.5.46	FHI 17333

(*Continued*)

Appendix 1. (*Continued*).

Species	Name of collector	Date of collection	Herbarium No.
	M. G. Latilo	27.5.69	FHI 62572
	,,	17.11.68	FHI 62292
	P. Wit and B. O. Daramola	28.12.71	FHI 64875
	Amachi	July 1958	FHI 3288
	J. Redhead	13.11.62	FHI 46387
	G. Ibhanesbhor	21.6.82	FHI 95397
	P. P. C. van Meer	24.8.65	FHI 92351
	Ariwaodo, J. A.	17.5.83	FHI 10042
	A. J. M. Leeuwenberg	10.3.65	FHI 68618
	Adebusuyi and Emwiogbon	24.8.63	FHI 45927
	J. Redhead	28.7.43	FHI 4127
	,,	24.10.52	FHI 48670
	Odewo, Ibhanesbhor and Oguntayo	9.7.79	FHI 90843
	Daramola and Osanyinlusi	23.4.79	FHI 90209
	L. Lowe	29.5.68	FHI 10781
	B. O. daramola and Kadiri A. B.	2.12.10	LUH 3291
M. cissoides Planch. ex Benth.	S. Tamajong	28. iv. 1946	FHI 16925
	Ekwuno et al.	15.9.81	FHI 95973
	J. K. Morton	7.11.52	FHI 48658
	Eimujeze and Oguntayo	28.5.74	FHI 72598
	Magbagbeola and Ariwaodo	26.6.81	FHI 94733
M. foetida Schumach.	J. K. Morton	24. 10.1952	FHI 48668
	J. A Emwiogbon	14.6.83	FHI 94993
	,,	7.7.66	FHI 60210
	J. Olorunfemi	12.10.59	FHI 43702
	P. Witt	25.8.71	FHI 26866
	J. Lowe	31.10.73	FHI 69287
	J. J. Bos	31.3.70	FHI 91488
	J.K. Morton	14.2.64	FHI 48668
	Dundas	10.3.47	FHI 20373
	Hall H. R.	11.10.49	FHI 27014
	A. J. M. Leeuwenberg	13.10.65	FHI 69463
	Gbile, Wit and Daramola	11.5.72	FHI 65588
	J. Redhead	13.11.62	FHI 46388
	Kadiri A. B.	26.7.12	LUH 5382
	,,	4.8.2007	LUH 603
	,,	29.6.09	LUH 225
M. multiflora Hook.f.	*C. F. A. Onochie*	26. vi.1957	FHI 31240
	,,	20.5.57	FHI 38776
	A. J. M. Leeuwenberg	3.7.65	FHI 69498
	Hall and Agyakwa	27.4.68	FHI 23612
	John Tangbo	23.9.76	FHI 94992
	J. J. Bos	7.7.70	FHI 97428
	Nditaph	30.11.59	FHI 50292
	A. P. D. Jones and R. W. J. Keay	9.10.45	FHI 13718
	M. G. Latilo	18.10.59	FHI 43482
	Ghesquire, J	Sept. 1937	FHI 19207
	J. K. Adebusuyi	22.6.62	FHI 45909
	Ogu	24.8.60	FHI 51283
	Dundas	30.12.45	FHI 13922
	Emwiogbon and Osanyinlusi	4.10.77	FHI 87029
	,,	4.10.77	FHI 87030
	,,	8.10.77	FHI 87141
	Z. O.Gbile and B. O. Daramola	31.3.70	FHI 62854
	Z. O. Gbile	20.7.70	FHI 67454
	Ariwaodo, J. A.	29.6.83	FHI 101882
	E. E. Zamierowskii	12.8.65	FHI 57568
	J. F. Redhead	4.11.64	FHI 5617
	Eimunjeze V. E and Binuyo A.	28.7.67	FHI 60599
	Olorunfemi and Oguntayo	29.11.77	FHI 86939
	B. O. Daramola and P. Ekwuno	14.7.70	FHI 67313
	Odewo, Ibhanesbhor and Oguntayo	16.6.79	FHI 90847
	B. O. Daramola	4.1.78	FHI 84524
	B. O. Daramola	26.7.79	FHI 91196

(*Continued*)

Appendix 1. (*Continued*).

Species	Name of collector	Date of collection	Herbarium No.
	Gbile, Olorunfemi and Binuyo	7.2.69	FHI 20582
	Oguntayo and Adejinmi	21.6.77	FHI 83340
	,,	21.6.77	FHI 90766
	T.K. Odewo	19.8.77	FHI 87969
	,,	25.8.77	FHI 91038
	Soladoye and Ekwuno	28.10.77	FHI 84073
	Peter and others	25.6.86	FHI 103443
	Oyayomi and Osanyinlusi	21.6.77	FHI 83396
Luffa aegyptiaca	*Anisere A.*	27.9.13	LUH 5919
	Lamidi R.	2.8.13	LUH 5995
	Kadiri A. B.	7.5.2010	LUH 3945
	B. O. Daramola	1.11.2008	LUH 581
	Ogaga A.	12.7.13	LUH 5890
	Tijani G.	21.11.12	LUH 5431
	Anigbogu O. J	2.2.07	LUH 1682
	Jaboro E.		LUH 3034
	Kehinde O.		LUH 582
	Kadiri A. B.	13.12.14	LUH 6354
	,,	15.12.14	LUH 6355
Trichosanthes cucumerina	*Olowokudejo J. D.*	19.11.2009	LUH 6357
	Kadiri A. B.	5.8.07	LUH 710
	,,	14.12.09	LUH 2053
	,,	9.3.10	LUH 1725
	Azeta O.	10.10.14	LUH 6257
	Kadiri A. B.	18.11.14	LUH 6356